Role of environment in dieback of jarrah: Effects of waterlogging on jarrah and *Phytophthora cinnamomi*, and infection of jarrah by *P. cinnamomi*.

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Abstract

The association of jarrah deaths with poorly drained dieback sites, following exceptionally heavy rainfall, indicates that hypoxic and anoxic soil conditions, which develop when soil is saturated, may be important in determining why jarrah dies. Experimental work has shown that when jarrah seedlings are waterlogged, xylem vessels in the tap root embolise and are sealed off with tyloses, thus root conductivity is suddenly reduced. Growth and development of *Phytophthora cinnamomi* are also affected because sporulation and vegetative growth are reduced under anaerobic conditions. When jarrah seedlings are inoculated with zoospores, more lesions form on roots in waterlogged soil than on roots maintained in moist soil.

Predictions from these experiments are that in the jarrah forest, soil saturation may directly affect jarrah roots by firstly reducing the number of functional vessels in the sapwood; secondly it will decrease sporulation of *P. cinnamomi* but thirdly will increase the probability of root infection. Less efficient roots and increased infection will affect tree growth and survival.

Introduction

Although 14.2 percent of the jarrah forest is infested by *Phytophthora cinnamomi* (Davison & Shearer 1989), jarrah does not invariably die on all infested (dieback) sites. Groups of trees die suddenly and spectacularly weeks or months after exceptionally heavy rainfall. Groups of jarrah deaths in the late 1940's followed the exceptionally wet winters of 1945-1948 (Harding 1949; Waring 1950), deaths in the late 1950's followed exceptionally heavy summer and winter rainfall in 1955 (Podger *pers. comm.*), deaths in the mid 1960's followed the exceptionally wet winters of 1963-1964 (Podger 1968) and deaths in 1982 followed exceptionally heavy rainfall in January 1982 (Shea *et al.* 1982).

These mass collapse sites, *i.e.* dieback sites where jarrah trees of all sizes and ages die suddenly, are in water gaining situations or are on soils with impeded drainage (Podger *et al.* 1965; Shea *et al.* 1982; Wallace & Hatch 1953; Waring 1950), not on high quality sites with deep, well drained soil profiles (Waring 1950). This association of jarrah deaths with poorly drained sites after periods of excessive rainfall implies that mass collapse occurs on sites in which the soil profile is saturated or partly saturated in the occasional wet years. Thus soil saturation (waterlogging) is an important environmental factor which is associated with jarrah deaths, and which has the potential to affect jarrah, *P. cinnamomi* and root infection.

Symposium on Plant Diseases in Ecosystems:
Threats and impacts in south-western Australia.
Held on April 16, 1994, at Murdoch University, by the Royal Society of Western Australia and the Ecological Society of Australia.

Symptoms in jarrah and their physiological basis

When jarrah trees die on mass collapse sites, the whole crown turns brown within a few days (Podger *et al.* 1965; Shea *et al.* 1982). These symptoms indicate severe water deficiency which will result if any of the following occur, either singly or in combination: (i) excessive transpiration (*e.g.* following extremely hot weather), (ii) reduced water uptake by fine roots (*e.g.* because the soil has dried out or a large proportion of fine roots have been damaged by pests or pathogens), (iii) reduced conduction of water between fine roots and foliage (*e.g.* caused by mechanical damage or rotting of the sapwood).

Observations of individual jarrah trees prior to crown death shows that there is a rapid decrease in stem girth for several weeks or months before foliage dies (*e.g.* Fig 1; Davison & Tay *unpublished data*). New leaves may still be produced in the crown even though the stem shows symptoms of gradually drying out. The tree shows symptoms of undergoing severe water deficiency which occurs in the stem before the crown, implying that there is either reduced water uptake by fine roots, or there is reduced water movement between roots and foliage.

Water moves between the roots and foliage in sapwood, an outer annulus of lighter coloured wood (xylem). Microscopic examination of sapwood shows that it is largely composed of small, thick-walled cells which give wood its strength and rigidity, and large xylem vessels through which water moves. Xylem vessels are capillary tubes which, in jarrah, are up to 0.4 mm in diameter, and approximately 50 cm long (Davison & Tay *unpublished data*). In sapwood the majority of vessels conduct water, but a few may be non-

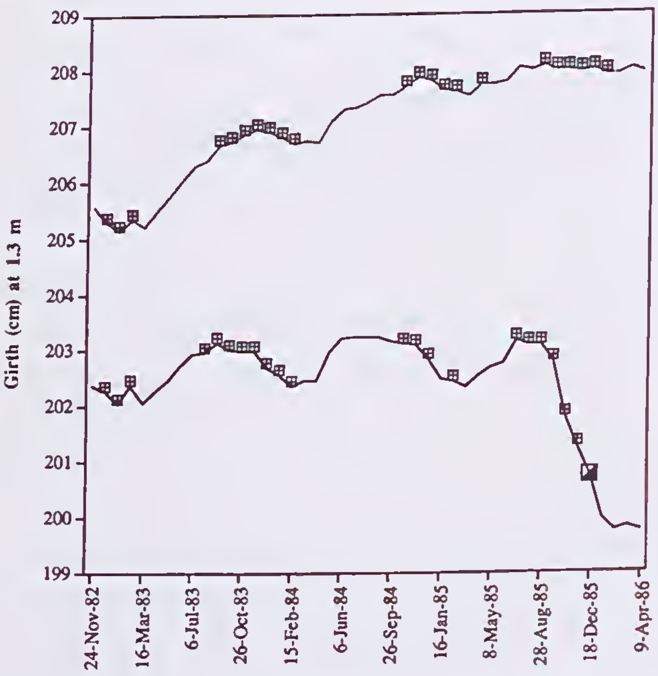

Figure 1. Comparison of girth changes at 1.3 m, leaf production and crown death in two mature jarrah trees of similar girth at Ross Block. One tree was in a dieback site, the other tree was in the adjacent uninfested area. Key: lower trace ——— tree 10, dieback site; upper trace ·········· tree 22, uninfested area; ⊞ young leaves present in the crown; ◢ crown death.

conducting, as indicated by ingrowths, tyloses, from adjacent cells. Tyloses only form in xylem vessels which are gas-filled, not water-filled (Zimmerman 1983). They are one mechanism by which a plant seals off damaged xylem, but it is not known what triggers their formation. Once tyloses form in a xylem vessel, that vessel will never conduct water, so that if there are large numbers of tylosed vessels in sapwood the conductivity will be reduced.

Effects of waterlogging on jarrah, *P. cinnamomi* and root infection

Experimental work

When soil is saturated with water, it becomes anaerobic because oxygen in the soil solution is rapidly consumed by micro-organisms and roots (Drew 1992). As oxygen diffuses 10^4 times more slowly through water than through air, it is used more quickly than it is replaced. Saturated soil will become hypoxic and anoxic more rapidly in summer than in winter, because the solubility of oxygen decreases with increasing temperature, and because respiration increases with increasing temperature. Laboratory measurements using jarrah forest soil show that, when saturated with water, it will become anoxic within 2 days at 20° C, and within 4 to 5 days at 16° C (Davison & Tay 1991). Anaerobic respiration is much less efficient than aerobic respiration so that, quite apart from any other physical and chemical changes in the soil, this sudden development of hypoxic and anoxic conditions is biologically very damaging.

Podger (1967) showed that jarrah was more sensitive to waterlogging than other forest eucalypts. Further work (Davison & Tay 1985) has shown that when jarrah seedlings are waterlogged under controlled conditions, xylem vessels in the tap root embolise and are sealed off with tyloses, so that roots become less efficient. This happens quickly; the proportion of tylosed vessels is correlated with the duration of waterlogging, and after 14 days at 20° C half of the vessels are blocked. Many woody plants close their stomata when their roots are waterlogged, but jarrah seedlings continue to transpire. Thus, the rate at which seedlings wilt and die depends on both the duration of waterlogging and the transpiration rate of the plants (Davison & Tay 1985).

Waterlogging also affects *P. cinnamomi*, a fungus which requires matric potentials close to zero for the production of sporangia, discharge and dispersal of zoospores (Gisi *et al.* 1980; Shea *et al.* 1983; Kinal *et al.* 1993). Sporulation, however, either does not occur or occurs very slowly under anaerobic conditions (Davison & Tay 1986). Zoospore germination is not affected by aeration, but germ tube growth is correlated with oxygen concentration (Davison & Tay 1986).

Infection of jarrah roots by zoospores of *P. cinnamomi* is greater in saturated soil than in soil at field capacity (Davison & Tay 1987). This is because more lesions are formed as a result of increased mobility of zoospores in flooded soil and increased attraction of zoospores to anaerobically respiring roots (Allen & Newhook 1973). Infection does not increase the proportion of occluded vessels in tap roots of jarrah seedlings (Davison & Tay 1987).

When large stems and roots are wound inoculated with *P. cinnamomi*, it preferentially colonises inner bark (Tippett *et al.* 1983; Davison *et al.* 1994). Although wound responses result in occlusion of xylem vessels adjacent to phloem lesions, this is of limited extent (Tippett & Hill 1984).

Field observations

Predictions for the field from the experimental work reviewed above are:

(i) if forest soil is waterlogged suddenly as a result of exceptionally heavy rainfall, the soil solution will rapidly become hypoxic and anoxic;
(ii) these conditions will not kill large jarrah roots, but will result in xylem vessels cavitating and becoming occluded with tyloses, so that these roots are less efficient at conducting water;
(iii) after the soil has drained, new functional xylem vessels will be formed by the root cambium. Thus, over time, the tylosed vessels in the sapwood will be replaced by newly formed vessels;
(iv) if there are seasonally high watertables in soil, large jarrah roots will be restricted to well aerated, surface horizons, so that jarrah trees on such sites will have shallow root systems;
(v) when the soil temperature is above 15°C and the matric potential is close to zero, *P. cinnamomi* sporangia will be formed on root lesions;
(vi) sporangia will not be formed below a watertable because aeration is inadequate, but will be formed in the moist soil above;
(vii) zoospores released from sporangia will move passively in percolating water through the profile into saturated soil where they will be attracted to, and infect, anaerobically respiring roots;

(viii) root infection will be more frequent in saturated soil than in moist soil;
(ix) the main tissue invaded will be the phloem;
(x) reduced hydraulic conductivity of root xylem will reduce the movement of water from the soil to the canopy, while increased infection of root phloem will reduce the movement of photosynthate and hormones from the crown to the roots;
(xi) both reduced hydraulic conductivity and increased infection will adversely affect tree growth.

Some of these predictions can be compared with field data.

Field measurements of perched watertables at Dawn Creek (Nanga Block) in June after 50 mm rain in the previous 4 days showed that the oxygen concentration of the soil solution was 49 per cent of water saturated with air (Davison & Tay 1991). Thus, perched watertables rapidly become hypoxic.

When jarrah dies on such sites, one would expect to find roots with large numbers of tylosed vessels in the sapwood, and extensively infected roots. Past investigations of jarrah deaths have included both anatomical and pathological studies (Table 1). Large numbers of tyloses were noted by Harding (1949), Stahl & Greaves (1959), Dell & Wallace (1981) and Davison (1993). *P. cinnamomi* lesions have not been found consistently, although failure by Harding (1949), Stahl & Greaves (1959), Podger (1968, 1972), Dell & Wallace (1981) and Shearer *et al.* (1981) to find lesions on vertical roots might be a result of incomplete root excavations (Table 1).

Table 1
Observations on tyloses and *Phytophthora cinnamomi* in jarrah trees.

Investigator(s)	Anatomical study		Pathological investigations	
		Tyloses noted	Consistent and extensive lesions	*Phytophthora* isolated
Harding (1949)	Yes	Yes	No	No
Stahl & Greaves (1959)	Yes	Yes	No	NA
Podger (1968, 1972)	NR	NR	NR	Yes
Dell & Wallace (1981)	Yes	Yes	Yes	Yes
Shearer, Shea & Fairman (1981)	NR	NR	Yes	Yes
Shea, Shearer & Tippett (1982)	NR	NR	Yes	Yes
Davison (1993)	Yes	Yes	No	No

NR, not reported; NA, not attempted

The most recent investigation of dying jarrah trees in a mass collapse site included the assessment of surface and sinker roots for both infection and tylosed sapwood (Davison 1993). No *P. cinnamomi* lesions were found. The mean proportion and standard deviation (calculated from arcsine-

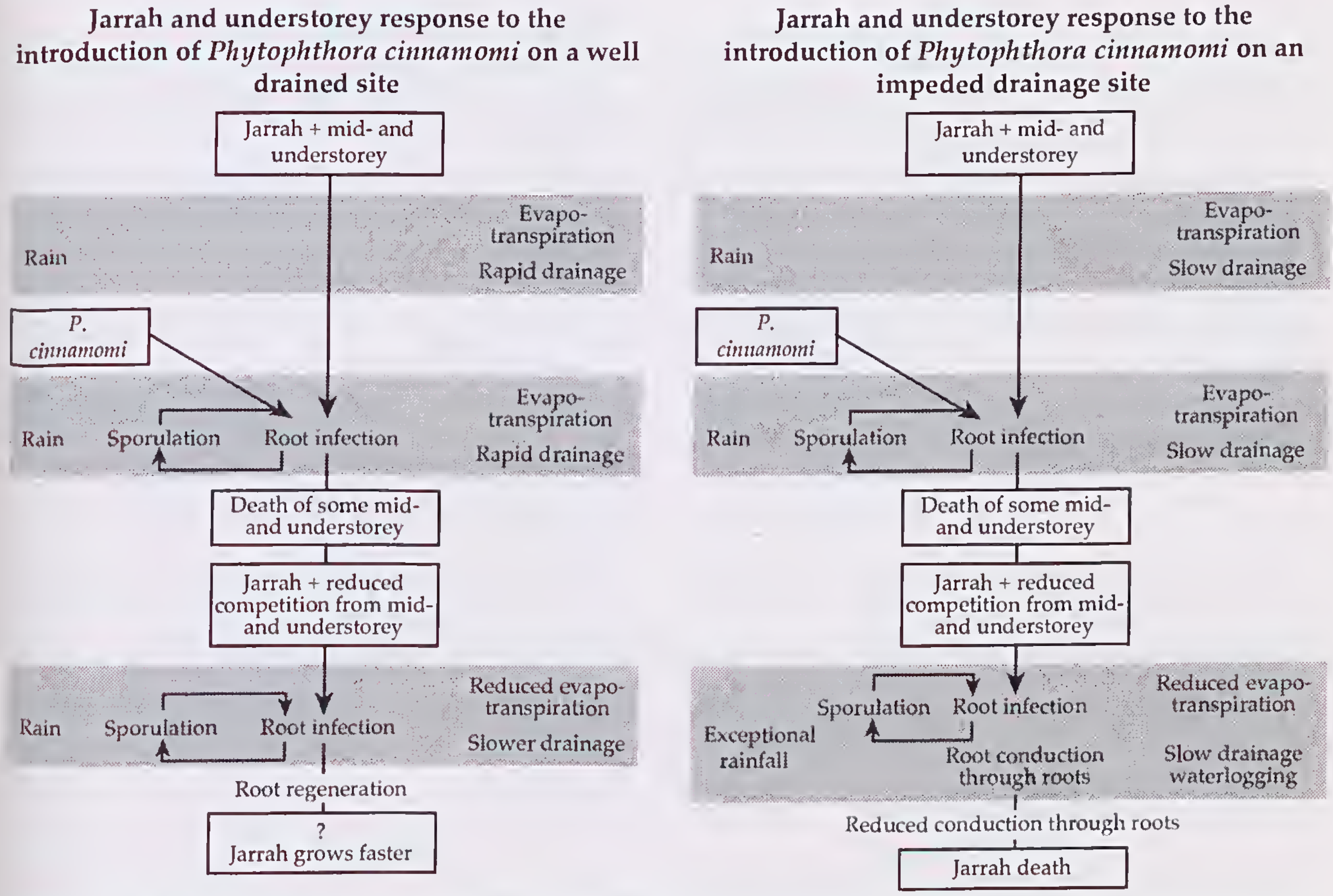

Figure 2. Hypothesised responses of jarrah and understorey to the introduction of *P. cinnamomi* on a well drained and an impeded drainage site.

transformed data) of tylosed vessels in 18 sinker roots was 74.8 per cent (standard deviation 44.2-96.3 per cent), and the mean proportion of tylosed vessels in 25 surface roots was 24.6 per cent (standard deviation 0.8-66.1 per cent). The proportion of tylosed vessel in the sapwood of surface roots from live trees from two other sites was 12.6 per cent (standard deviation 1.3-31.3 per cent, n=201), calculated from arcsine transformed data (Davison & Tay *unpublished data*).

Another prediction from experimental work is that there would be more lesions on roots of jarrah trees growing on poorly drained sites than on well drained sites. In excavations of apparently healthy trees growing on infested sites, Shearer & Tippett (1989) recovered *P. cinnamomi* from only 4.7 per cent of large roots. Similarly Davison & Tay (*unpublished data*) only found *P. cinnamomi* lesions on 3.4 per cent of 44 large roots from two sites which differed in soil drainage. In this latter study, lesions were too infrequent for statistical analysis.

Quite apart from its ability to infect jarrah, *P. cinnamomi* kills many mid-and understorey plant species (Podger 1968). By reducing vegetation density, it will reduce both interception of rainfall and evapotranspiration from the site (Greenwood *et al.* 1985). These changes will have a major effect on site hydrology, so that dieback sites will be wetter than adjacent uninfested areas. If site topography and/or soil profile characteristics result in poor drainage, this will be exacerbated by a removal of vegetation. Thus there will be an increase in both the incidence and duration of waterlogging on such sites in the occasional wet years (Fig 2).

Conclusions

In any investigation in plant pathology it is important to know as much about the host as about the pathogen. With studies of *P. cinnamomi* this may be conceptually difficult because this fungus has such a wide host range that it is natural to concentrate on the pathogen rather than on the many species affected, which in turn can affect the whole ecosystem. *Phytophthora cinnamomi* does not just infect plants, it also has a dramatic effect on site hydrology by reducing vegetation density. It is also important to consider how associated environmental factors affect the known physiological limitations of both host and pathogen because this may provide insights into how to predict when and where deaths will occur, and how to reduce their incidence.

Acknowledgments: I thank I Colquhoun, G Hardy and other colleagues whose comments have improved this manuscript.

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